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The Systematic Status of *Perognathus artus* and *Perognathus goldmani* (Rodentia)

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In 1900, W. H. Osgood described and named *Perognathus artus* and *Perognathus goldmani*, two new species of pocket mice belonging to the *intermedius* group of species of the subgenus *Chaetodipus*. Both of the new species inhabited the coastal plain of western Mexico. *Perognathus artus* was then represented by 15 specimens from three localities, and *Perognathus goldmani* was represented by 36 specimens from three other localities.

In 1938, W. H. Burt reported additional specimens of *P. artus*, from Guirocoba, Sonora, and *P. goldmani*, from Tesia and Chinobampo, Sonora. In 1941, Burt and Hooper reported both species from one locality, Carimechi, Chihuahua. In 1959, Hall and Kelson mapped non-overlapping ranges for the species. In 1960, Hall and Ogilvie reported that they judged the two species to be conspecific. Their report listed 157 specimens of *P. artus* examined and 66 of *P. goldmani*, and they mapped 23 localities.

Study of recently collected material in several institutions and restudy of older material have provided new information on distribution and variation and have led me to the conclusion that *P. artus* and *P. goldmani* are separate species. In the preparation of the present report 316 specimens of *P. artus* and 238 specimens of *P. goldmani* were studied.

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A grant from the National Science Foundation (G 10874) helped me in the early part of this study. Continued diligent work in northwestern Mexico by Messrs. M. Raymond Lee and Percy L. Clifton and other persons from the University of Kansas, with support obtained from the National Science Foundation and other sources by Prof. E. Raymond Hall, has resulted in my obtaining the critical material needed to resolve the problem. I am grateful to Professor Hall and Dr. J. Knox Jones, Jr., for making this material available. Specimens in the following collections have been used, and the assistance of the curators noted is gratefully acknowledged: the American Museum of Natural History (A.M.N.H.); Museum of Natural History, University of Kansas, Lawrence (K.U.); Dr. E. Lendell Cockrum, University of Arizona, Tucson (U.A.); Mr. O. Marcus Buchanan, the Donald R. Dickey Collection, University of California, Los Angeles (U.C.L.A.); Dr. Donald F. Hoffmeister, Museum of Natural History, University of Illinois, Urbana (U.I.); Drs. William H. Burt and Emmet T. Hooper, Museum of Zoology, the University of Michigan, Ann Arbor (U.M.M.Z.); and Drs. David H. Johnson and Richard H. Manville, United States National Museum of the Smithsonian Institution, including the Biological Surveys Collection (U.S.N.M.). The initials in the above list are used in the paragraphs concerning the specimens examined to designate the various collections.

Graphs, maps, and drawings in figures 1 through 56 were initially plotted or drawn by the author and then completed in the Department of Graphic Arts of the American Museum. Credits for photographs are given in the legends for figures 57 through 61.

Differences in specimens resulting from differences in age, sex, and geographic origin have been noted. Geographic variation has genetic and environmental components. The genetic component may have arisen through evolution in response to environmental factors. In most taxonomic studies there is no method by which these components can be clearly distinguished. Local and ontogenetic environmental effects probably rarely result in incorrect taxonomic judgments when adequate series of specimens taken at different places, in different years, by different collectors, and under different climatic conditions, are available, as I have previously commented at greater length (Anderson, 1959, p. 432). A knowledge of variation from all sources is important in intraspecific study, and in the reaching of decisions about the systematic status of closely related forms, such as the species of *Perognathus* under consideration.

Specimens in this study have been placed in five groups according to relative ages as judged from wear on the teeth. These age groups are as follows:

1. Upper deciduous premolar still present
2. Upper permanent premolar erupted but unworn
3. All teeth worn, first two molars still bilobate (this stage of wear is shown in fig. 58)
4. Most of the major fold of at least one of the first two molars worn away
5. All molars reduced to dentine-filled enamel lakes

Age groups 3, 4, and 5 are combined in the samples analyzed. The mean of the age groups was computed for each sample so that differences could be considered in evaluating significance of mean differences in other measurements. There is an average increase of about 0.5 mm. in occipitonasal length between age groups 3 and 4 and between age groups

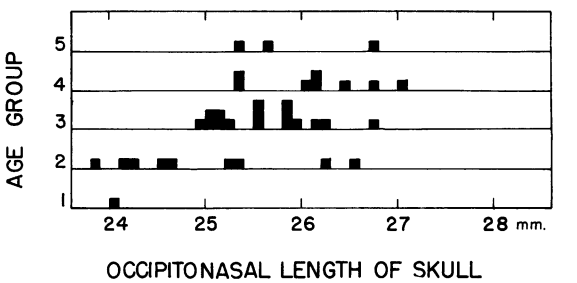


FIG. 1. Graph showing frequency distribution of occipitonasal lengths of skulls in each of five age groups of *Perognathus artus*. All suitable Chihuahuan specimens are included. The average difference between adjacent age groups is about 0.5 mm., and the difference is greater between younger age groups. Age groups 3, 4, and 5 were combined for statistical calculations in this study.

4 and 5. The frequency distribution for all Chihuahuan specimens of *P. artus* is shown in figure 1. In this pooled sample the range of variation of about 2 mm. within each of the three oldest age groups is less than in most samples, including those from single localities, in which a range of about 3 mm. is common.

The average size of males is larger than that of females. If samples of more than five adults are considered, about eight of 10 samples will have a male as the largest individual. The sample with the largest number of individuals of age group 4 is sample I (see fig. 2). Measurements of the occipitonasal length of these are: males, $N=4$, 27.67 (26.8–29.2); females, $N=7$, 26.81 (25.1–28.0). Although these means are not significantly different (t 2.19), it is safe to assume that larger samples would reveal a significant difference in spite of much overlap in ranges (see also figs. 59 and 60). Males and females have been combined in the samples that were used in the study of geographic variation. The percentage of males

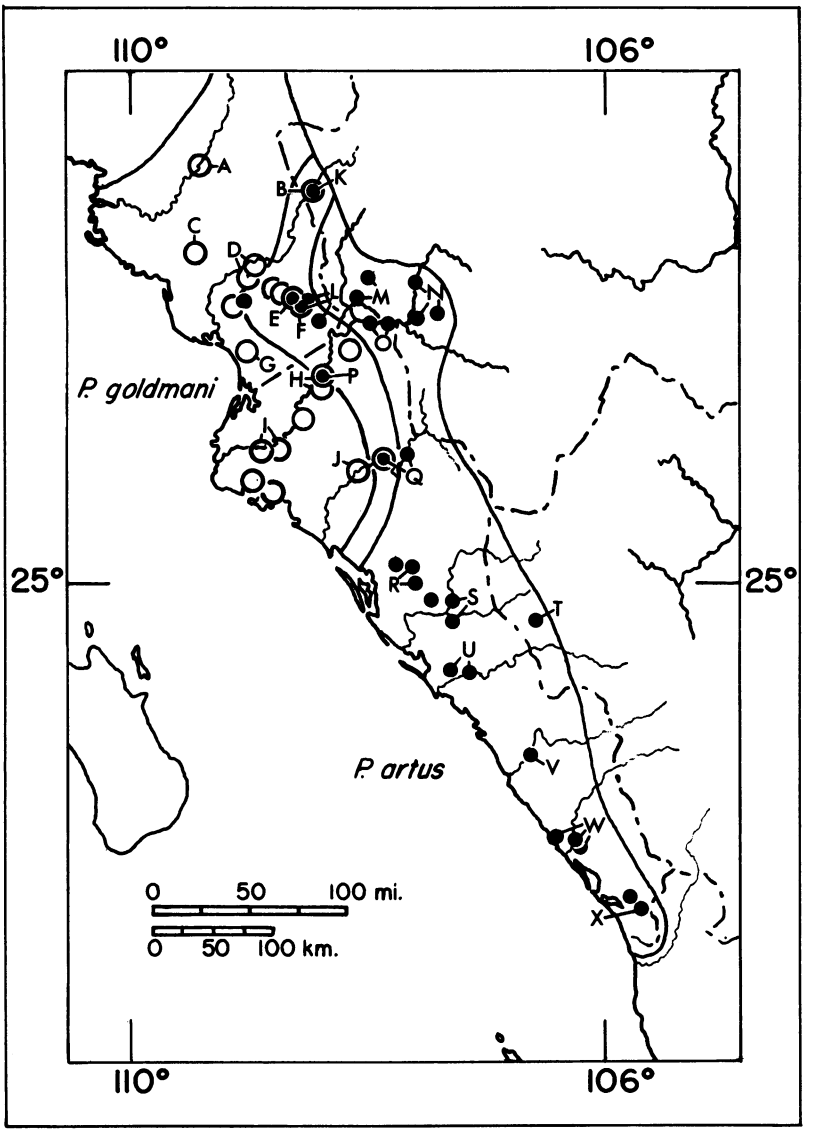


FIG. 2. Map of the distributions of *Perognathus artus* and *Perognathus goldmani* in Sinaloa, Chihuahua, Durango, and southern Sonora. *P. goldmani* extends north of the area mapped in Sonora, although no specimens from there were used in this study. Each letter, A to X, indicates a locality or localities, from which a sample used for statistical purposes was derived. Circles indicate localities where *P. goldmani* occurs; dots, those where *P. artus* occurs. A zone of geographic overlap is indicated, within which are several localities where both species are known to occur.

TABLE 1

EXTERNAL MEASUREMENTS (IN MILLIMETERS) OF ADULT *Perognathus*

(For each measurement and each group the mean and standard deviation are followed by the minimum and maximum, in parentheses. A "group" is a sample from a locality or localities shown by a corresponding letter in fig. 2. Some data are omitted for small samples.)

Group	*N*	Total Length		Length of Hind Foot	
P. goldmani					
A	2	190	(185–194)	25.5	(25–26)
B	1	214		24	
C	2	190	(185–195)	25	(25–25)
D	28	186.5±8.2	(172–199)	24.9±1.1	(23–27)
E	31	180.0±7.3	(160–192)	24.7±0.9	(23–26.5)
F	8	183.5±8.1	(170–196)	24.2±0.7	(23–25)
G	12	191.2±7.3	(179–201)	25.0±0.7	(24–26)
H	11	194.4±13.3	(176–218)	24.8±0.9	(23–26)
I	25	197.6±4.3	(168–236)	25.0±1.0	(23–27)
J	20	196.1±6.7	(187–210)	26.4±1.1	(25–29)
P. artus					
K	2	182	(182–182)	23.5	(23–24)
L	18	177.4±7.4	(166–190)	23.2±0.6	(22–24)
M	5	179.5	(169–200)	21.6	(21–22)
N	14	179.9±9.7	(160–197)	23.5±1.0	(22–25.5)
O	9	178.2±8.3	(165–195)	23.2±1.6	(21–25)
P	9	177.9±10.3	(165–201)	23.6±0.7	(23–25)
Q	11	171.1±8.8	(159–182)	23.1±0.9	(21.5–25)
R	16	180.6±9.0	(168–204)	23.2±0.9	(21–24)
S	21	184.5±8.3	(169–197)	23.6±0.8	(22–25)
T	3	171.3	(154–182)	23.7	(22–25)
U	16	183.3±13.5	(165–218)	23.6±1.2	(22–26)
V	1	167		21	
W	6	161.5±6.3	(150–170)	22.4±0.2	(22–22.5)
X	1	160		21	

in each sample has been calculated. Both *P. artus* and *P. goldmani* vary with age and sex, as noted above.

In the evaluation of the significance of differences, it may be assumed as an approximation that the average difference in occipitonasal length of skull between samples entirely of females and those entirely of males is 1 mm. Then, for example, the mean of a sample that includes 70 per cent of males may be assumed to be 0.2 mm. greater than that of a sample from the same population including equal numbers of each sex.

Male and female specimens of age groups 3, 4, and 5 were combined

TABLE 2

CRANIAL MEASUREMENTS (IN MILLIMETERS) OF ADULT *Perognathus*

(For each measurement and each group the mean and standard deviation are followed by the minimum and maximum, in parentheses. A "group" is a sample from a locality or localities shown by a corresponding letter in fig. 2. Some data are omitted for small samples.)

Group	*N*	Average Age Group	Per Cent of Males	Occipitonasal Length	Mastoidal Breadth	Bullar Length
P. goldmani						
A	2	3.0	100	28.0 (26.8–29.1)	13.6 (13.3–13.9)	7.0 (6.8–7.1)
B	1	3	100	26.5	12.5	—
C	3	3.3	33	26.63 (26.2–27.2)	13.30 (13.1–13.4)	6.57 (6.4–6.8)
D	28	3.3	64	26.85±0.67 (25.8–28.2)	13.82±0.35 (13.3–14.5)	6.75±0.36 (6.2–7.5)
E	31	3.4	61	25.97±0.64 (24.5–27.0)	13.10±0.33 (12.6–14.1)	6.51±0.37 (5.8–7.2)
F	9	3.1	44	26.73±0.89 (24.7–27.7)	13.52±0.37 (12.9–14.0)	6.63±0.18 (6.4–6.9)
G	12	3.8	42	26.71±0.71 (26.0–28.4)	13.71±0.38 (12.9–14.4)	6.63±0.28 (6.2–7.1)
H	11	3.4	36	27.20±0.71 (26.1–28.6)	13.78±0.36 (13.3–14.3)	6.93±0.26 (6.5–7.4)
I	26	3.6	38	27.40±1.41 (25.1–31.4)	13.96±0.55 (12.6–15.2)	6.70±0.45 (5.9–8.0)
J	20	3.1	50	28.15±0.53 (27.2–29.3)	13.96±0.30 (13.5–14.4)	7.22±0.35 (6.5–7.7)

TABLE 2—(*Continued*)

Group	*N*	Average Age Group	Per Cent of Males	Occipitonasal Length	Mastoidal Breadth	Bullar Length
P. artus						
K	2	3.5	100	26.35 (26.0–26.7)	12.05 (12.0–12.1)	—
L	19	3.4	63	26.10±0.80 (24.8–27.1)	12.83±0.30 (12.4–13.3)	5.57±0.23 (5.2–6.1)
M	5	3.6	40	26.00 (25.3–26.7)	12.46 (12.1–12.9)	5.32 (4.9–5.9)
N	21	3.5	38	25.70±0.61 (24.9–27.0)	12.51±0.31 (12.0–13.3)	5.52±0.18 (5.2–5.9)
O	9	3.7	44	25.70±0.81 (24.4–27.1)	12.43±0.21 (12.1–12.8)	5.77±0.33 (4.9–6.1)
P	9	3.6	44	25.97±0.81 (25.2–27.7)	12.32±0.31 (12.0–12.8)	5.79±0.33 (5.3–6.4)
Q	12	3.2	58	25.82±1.05 (24.6–28.4)	12.47±0.37 (11.8–12.9)	5.98±0.39 (5.5–6.5)
R	18	3.5	44	26.58±0.97 (25.3–28.9)	13.19±0.48 (12.5–14.6)	5.87±0.33 (5.1–6.5)
S	22	3.8	64	26.33±0.83 (25.1–28.0)	13.07±0.33 (12.5–13.5)	5.68±0.28 (5.1–6.1)
T	2	4.0	50	26.35 (26.3–26.4)	12.45 (12.4–12.5)	5.35 (5.2–5.5)
U	19	3.4	47	26.88±0.96 (25.0–28.9)	13.36±0.37 (12.7–14.0)	6.03±0.27 (5.5–6.7)
V	1	3	100	25.1	12.6	5.2
W	8	3.4	38	24.84±0.68 (24.2–26.2)	12.62±0.32 (12.2–13.0)	5.39±0.28 (5.1–5.7)
X	1	3	0	23.9	12.7	5.2

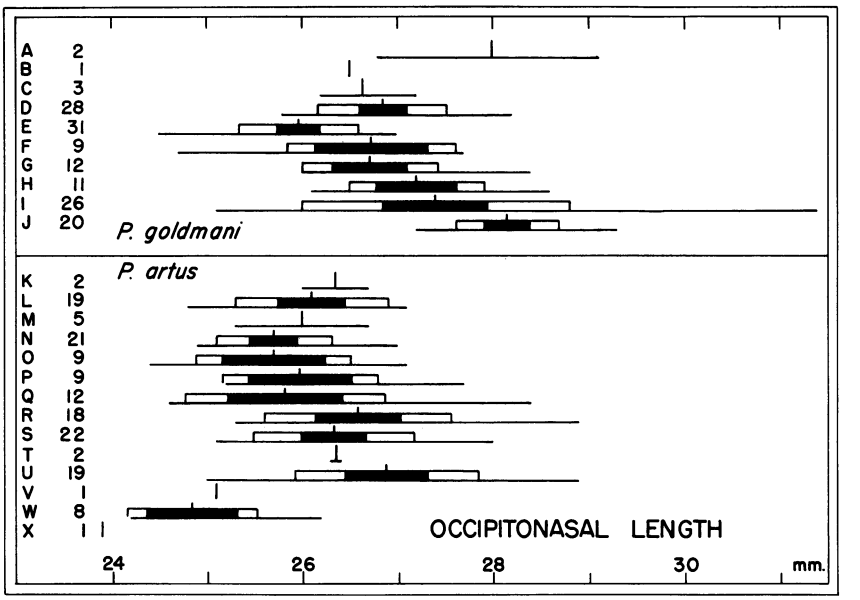


FIG. 3. Graph showing statistical data for occipitonasal length of specimens of *Perognathus artus* and *Perognathus goldmani*. Samples A to X represent areas shown in figure 2. These areas are roughly arranged from north to south for each species. Numerals show sample sizes. Animals of both sexes and of age groups 3, 4, and 5 were used. For each sample the range is shown by a horizontal line; the mean, by a vertical line; one standard deviation each side of the mean, by boxes; and two standard errors each side of the mean are shown by a bar. Data are derived from table 2. A clinal trend toward larger size in more southern samples of *P. goldmani* is suggested. Only on the average, and not in all samples, does larger size distinguish *P. goldmani* from *P. artus*. The largest specimens of *P. artus* occur in samples R, S, and U from central Sinaloa; the smallest, in samples V, W, and X from southern Sinaloa. Possibly study of additional Sinaloan material will indicate the usefulness of dividing *P. artus* into three subspecies. I have not examined adequate material.

into 24 samples for statistical analysis of two external measurements and three cranial measurements. Some samples represent a single locality, and others represent several localities that were judged not to be separated by any significant barrier and that did not exhibit any apparent morphological differences. The localities represented in these 24 samples are indicated in figure 2. The data are given in tables 1 and 2, and cranial data are shown graphically in figures 3 and 4. The occipitonasal length is the greatest length of the skull from the supraoccipital bulge to the anterior end of the nasals. The mastoidal breadth is the greatest breadth

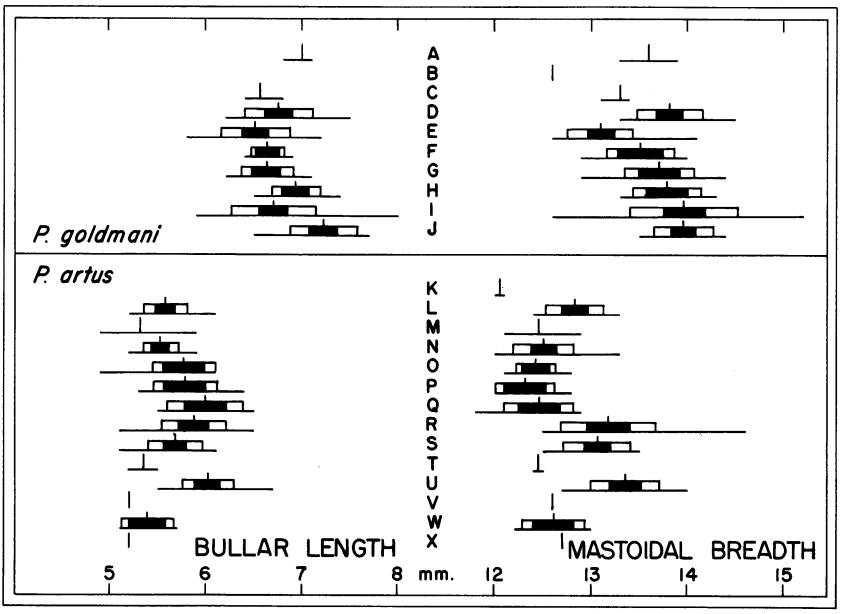


FIG. 4. Graphs showing statistical data for bullar length and mastoidal breadth of specimens of *Perognathus artus* and *Perognathus goldmani*. Samples A to X are from localities shown by the same letters in figure 2 and are the same samples on which figure 3 is based. Data are derived from table 2. For each sample the range is shown by a horizontal line; the mean, by a vertical line; one standard deviation each side of the mean, by boxes; and two standard errors each side of the mean are shown by a bar. Methods of measurement are described in the text. The bullar length is the best single cranial measurement to distinguish the two species. All mean values of *P. artus* are significantly smaller than those of *P. goldmani*, and, even when these measurements overlap, the bullae themselves are distinguishable on the basis of ridging, surface texture, size relative to other parts of the skull, and other features noted in the text. Mastoidal breadth is less diagnostic than bullar length, but more diagnostic than occipitonasal length.

of the skull measured between the lateralmost points of the mastoid bones (not between the squamosal ridges when these extend beyond the mastoids as is often the case in *P. artus*). The bullar length is an oblique measurement of the exposed mastoid bone from the point where the transverse ridge intersects the mastoid-supraoccipital suture to the most distant point on the anterior margin of the mastoid. Measurements were all taken with dial calipers and recorded to the nearest tenth of a millimeter. These three measurements were selected as best representing the size of the skull and the differences between *P. artus* and *P. goldmani*.

Osgood (1900, p. 54) compared *P. goldmani* with *Perognathus nelsoni*,

"its nearest relative." He noted that specimens of *P. goldmani* from Sonora were slightly smaller than those from Sinaloa. *Perognathus artus* was said to differ from *P. goldmani* in having (1) "weak or undeveloped" rump bristles, (2) a smaller and (3) narrower skull, (4) smaller mastoids with (5) more strongly marked transverse ridges, (6) smaller audital bullae, and (7) nasals exceeded posteriorly by the ascending processes of the premaxillae.

Burt and Hooper (1941, p. 6) noted in reference to specimens from Carimechi, Chihuahua, that *P. artus* was (8) slightly smaller externally, and had (9) a less hairy tail and (10) a broader dorsal tail stripe than *P. goldmani*. In the skull, the supraoccipital was (11) broader in *P. artus* and characters 4, 5, and 7 were also observed. The mastoids were also said to be (12) more rugose in *P. artus*. Characters 1, 2, 3, and 6 were not mentioned by Burt and Hooper.

Hall and Ogilvie (1960) mention the difference in size (characters 2 and 8), the difference in inflation of the tympanic bullae (character 6), and an additional character (13), an interparietal that is relatively wider (transverse to long axis of skull) in *P. artus*. Other characters were not mentioned. Specimens from four localities in southeastern Sonora were said to exhibit an intergrading cline between *P. artus* and *P. goldmani* in size and in "features other than size." No measurements were cited, and no specific features other than size were noted. The four localities in southern Sonora cited by Hall and Ogilvie (1960, p. 515) are included in the areas from which my samples A, D, E, and L are drawn. The numbers of adults (age groups 3, 4, and 5, as described above) in the samples used by Hall and Ogilvie were one in sample A, five in sample D, five in sample E, and none in sample L. Their sample of five from 9 miles southeast of Alamos (part of my sample L) includes two in preservative, two of age group 2, and one that my notes do not show that I have ever seen (K.U. No. 80058). Occipitonasal lengths of their three samples in millimeters are A, 29.1; D, mean 26.48 (range of 26.1–27.0); E, 26.44 (24.7–27.7). Measurements of the two slightly younger individuals in sample L are 24.6 and 25.1. These measurements are not adequate to reveal any significant difference in size between samples D, E, and L, even though two species are represented. Larger samples that I have studied (see tables 1 and 2) indicate that most, but not all, samples of *P. goldmani* average larger than samples of *P. artus*, but that overlap in size is great and that neither individual specimens nor small samples can be certainly identified by the use of only the total length of the skull or of the entire animal.

Six specimens from 4 miles north of Terrero, Sinaloa, were judged by

Hall and Ogilvie to be intergrades between *P. goldmani* as represented by specimens from 10 miles north-northwest of Los Mochis, Sinaloa, and *P. artus* as represented by specimens from 1 mile south of Pericos, Sinaloa. Intermediacy in "length of hind foot, width of interparietal, and width of tympanic bullae," and in total length (nearer *P. artus*) and length of tympanic bullae (nearer *P. goldmani*) was indicated. In the lack of inflation laterally of the mastoidal bullae the specimens were said to "agree with *artus*." My sample I includes the locality designated from Los Mochis, and my sample R includes localities designated from both Pericos and Terrero. The last two series are referred to as the "Pericos series" and the "Terrero series" in the following discussion. The cards on which data used by Hall and Ogilvie were originally recorded were given to me by Mrs. Ogilvie. I have used their measurements in computing the mean, standard error, and range for each of the three samples and each of the five measurements cited as being intermediate in the presumed intergrades. For each measurement the first sample is from area I (*P. goldmani*), the second sample is the Terrero series (presumed intergrades), and the third is the Pericos series (*P. artus*). All measurements are in millimeters.

The following data for total length of these three series indicate that the means are not significantly different:

$N=12$, 193.7 ± 3.4 *S.E.* (168–207)
$N=5$, 185.6 ± 4.6 *S.E.* (172–198)
$N=10$, 184.1 ± 3.0 *S.E.* (168–204)

The following data for the length of the hind foot indicate that only the first and second means are significantly different (t 2.73):

$N=12$, 25.1 ± 0.3 (23–27)
$N=6$, 23.6 ± 0.4 (23–25)
$N=10$, 23.2 ± 0.3 (21–24)

Data for the width of the interparietal indicate that only the first and third means are significantly different (t 3.16):

$N=12$, 7.43 ± 0.11 (6.9–8.1)
$N=5$, 7.66 ± 0.28 (7.0–8.2)
$N=10$, 7.93 ± 0.11 (7.2–8.4)

Data for the length of the tympanic bullae indicate that all three means are significantly different (t for difference between first and second mean is 2.55, between the second and third t is 2.85):

N=12, 7.58±0.09 (7.0–8.0)
N= 5, 7.18±0.10 (6.8–7.5)
N= 8, 6.80±0.08 (6.5–7.2)

Data for the width of the tympanic bullae indicate that only the second and third means are significantly different (t 2.35):

N=12, 4.57±0.04 (4.3–4.8)
N= 5, 4.40±0.07 (4.3–4.6)
N= 8, 4.22±0.04 (4.1–4.4)

The means of the Terrero series are intermediate in each measurement; however, four of the five specimens in the Terrero series are males, and only four of 10 specimens in the Pericos series are males. Males average larger than females. When this fact is considered, there seems to be no reason to conclude that the Terrero series is significantly different from the Pericos series. In any case, interpretation of the data of Hall and Ogilvie as evidence of intergradation is questionable in view of the failure of several other characters to exhibit intermediacy.

The presumed intergrades in the Terrero series were said to average even larger than *P. goldmani* from 10 miles north-northwest of Los Mochis in occipitonasal length and mastoidal breadth, but not so large as *P. goldmani* from the type locality (Sinaloa, Sinaloa, erroneously stated to be farther north than the locality 10 miles north-northwest of Los Mochis). This statement is correct, but is neither statistically nor taxonomically significant. Occipitonasal measurements for the series from near Los Mochis, the Terrero series, and specimens from Sinaloa are:

N=12, 27.11±0.29 *S.E.* (25.0–28.5)
N= 5, 27.66±0.50 *S.E.* (26.0–28.9)
N= 6, 28.05±0.24 *S.E.* (27.2–28.9)

Mastoid breadth in these three series measured:

N=12, 13.85±0.14 (12.6–14.5)
N= 5, 13.96±0.26 (13.3–14.9)
N= 6, 14.10±0.08 (13.8–14.4)

In neither of the measurements are means significantly different at the 95 per cent confidence level.

The degree of inflation of the mastoidal bullae was said to vary geographically. As an example, the mastoidal bullae of the "25 specimens of *goldmani* from two and a half miles north of El Fuerte, Sinaloa," were said to be intermediate in size between those of *P. goldmani* and those of *P. artus*. No measurements were published to document reported differences, and the method of taking measurements or of making observations

of the bullae was not described. The "25 specimens of *goldmani* from two and a half miles north of El Fuerte, Sinaloa" were examined by me. Nine of them are from El Fuerte proper, and five of these are *Perognathus pernix*, not *P. goldmani*. The measurements of the bullae were recorded (on original data card) for six specimens. The mean length of the bullae is 7.41 (7.0–7.8). This mean is between the means for *P. goldmani* from near Los Mochis and those of *P. artus* from the Terrero series, but is not significantly different from either. On the basis of characters that are discussed below, the specimens from El Fuerte and from 2½ miles north of El Fuerte are clearly *P. goldmani*. A more recently obtained series from 3 miles northeast of El Fuerte includes both *P. artus* and *P. goldmani*, but no intermediate individuals.

We may conclude from the above analysis of the measurements and specimens reported by Hall and Ogilvie that the cited evidence is not inconsistent with the hypothesis of intergradation between *P. artus* and *P. goldmani*, but that the evidence does not prove intergradation or even indicate its probable occurrence. Additional evidence indicates that intergradation is not probable.

The 13 characteristics in which *P. artus* has been said by earlier authors to differ from *P. goldmani* are:

1. Rump bristles weak or undeveloped (see fig. 57)
2. Skull smaller, occipitonasal length used in testing this difference (see figs. 59 and 60)
3. Skull narrower, mastoid breadth used
4. Mastoid smaller in area anterior to transverse ridge (see fig. 58H)
5. Transverse ridge on mastoid more strongly marked
6. Audital (or "tympanic") bullae smaller, in ventral aspect
7. Ascending processes of premaxillae extend posterior to nasals a distance equal to or greater than the least breadth of one nasal bone (see fig. 58B, C)
8. Size smaller externally, total length measurement used
9. Tail less hairy, especially in distal third, but scalation more evident in basal part also (see fig. 57G–J)
10. Dorsal tail stripe broader, in dorsal view white not usually visible along sides
11. Supraoccipital broader, least supraoccipital breadth measured
12. Mastoids more rugose, more pits
13. Interparietal relatively wide, interparietal length at right angle to long axis of skull expressed as a percentage of mastoidal breadth

Subject to certain qualifications, these characters are all useful in distinguishing the two forms, and I would add to the list the following characters in which *P. artus* differs from *P. goldmani:*

14. Pelage darker
15. Pigmentation of ears darker

16. Dorsal pelage has slightly more uniform, less grizzled appearance (see fig. 57B, C)
17. Baculum shorter
18. Baculum more curved
19. Baculum thicker in proportion to length, especially distally
20. Base of baculum deflected ventrally
21. Lacrimal suture with maxilla and frontal, as viewed in dorsal aspect, longer than the length of the lacrimal from this suture to tip

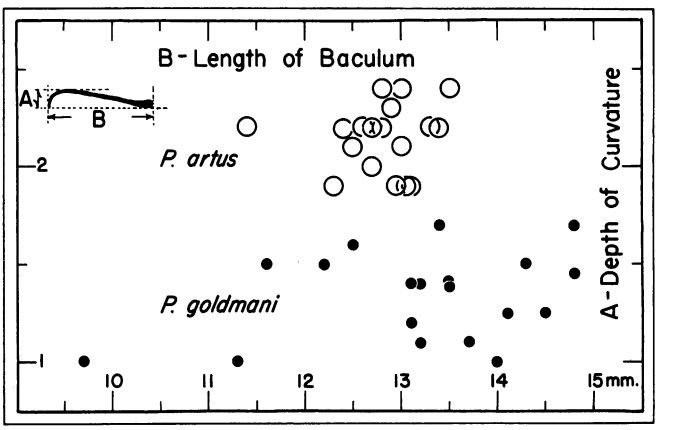


FIG. 5. Graph comparing the length of baculum with depth of curvature of the baculum in *Perognathus artus* and *Perognathus goldmani*. Inset figure at upper left shows the dimensions measured. Measurements were of drawings made to scale on graph paper. Bacula were viewed through a microscope while in glycerin and lying on a millimeter ruled grid. The bacula used are the intact specimens shown in figures 6 through 56. The bacula are from various parts of the ranges of each species. Every baculum studied could be identified to species.

22. Maxillo-frontal suture reaches farther posteriorly, relative to position of lacrimal
23. Jugal in dorsal view more slender
24. Temporal ridge less curved, lacking angular tuberosity on the anterior part of the squamosal
25. Skull shallower
26. Palatal pits deeper (see fig. 58I, J)
27. Exoccipital forms more distinct flange at the edge that meets the mastoid
28. Stylomastoid foramen larger, more conspicuous (see fig. 58H)

No single character will suffice to identify every specimen, and some characters differ only on the average and not in all samples. When several characters are used, however, every specimen can be identified. Each of 51 bacula that I have studied is identifiable (see figs. 6–56), but females, having no bacula, are of course not identifiable by characters 17 to 20.

Females average slightly smaller than males but were not observed to be different from males in other characters studied. Measurements have not been devised for all characters. Some characters that can be easily observed would be difficult to measure, for example, the rugosity or degree of pitting of the dorsal exposure of the mastoid.

To indicate the relative reliability of the different characters, three different pairs of series were compared for each of the 28 characters. Specimens of *P. artus* from Urique, Chihuahua (within my sample area N), were compared with specimens of *P. goldmani* from 10 miles north-northwest of Los Mochis, Sinaloa (part of sample I). Specimens of *P. artus* from 9 miles southeast and 9 miles east-southeast of Alamos, Sonora (in sample L) were compared with specimens of *P. goldmani* from 1 mile distant, 10 miles southeast of Alamos (in sample F). Finally, *P. artus* from the Terrero series and the Pericos series in Sinaloa (together comprising sample R) were compared with *P. goldmani* from 13 miles north-northeast of Los Mochis, Sinaloa (part of sample I). In each comparison an arbitrary intermediate condition, either an actual measurement or a certain specimen for comparison, was selected. All specimens were compared with this standard, and the number of specimens that would be correctly identified with the use of this one character was recorded.

The results of these comparisons, expressed as percentages of individuals correctly identified with the use of each character alone, are as follows:

Character	Samples N and I	Samples L and F	Samples R and I
1	100	100	96
2	95	85	89
3	95	77	94
4	100	100	100
5	95	100	89
6	100	62	82
7	100	77	88
8	96	81	100
9	83	81	100
10	59	69	93
11	60	77	65
12	80	100	94
13	70	92	100
14	83	100	97
15	75	88	60
16	83	100	100
21	100	100	81
22	100	92	69
23	100	85	65
24	90	100	72

Character	Samples N and I	Samples L and F	Samples R and I
25	100	85	83
26	80	77	82
27	95	100	56
28	100	100	67
Average of all values	89	88	84

The characters of the bacula (17 to 20) were not included because of smaller samples. All intact bacula of *P. artus* were compared with all those of *P. goldmani* for each of the four characters, with the following results:

Character 17, 64 per cent correctly identified
Character 18, 100 per cent correctly identified
Character 19, 90 per cent correctly identified
Character 20, 90 per cent correctly identified

See figures 6 through 56, which illustrate most of the bacula that were studied.

Samples L and F, representing the two species at localities 1 mile apart in southern Sonora, are as distinct from each other as are samples N and I, representing the two species at localities about 115 miles apart and away from areas of potential intergradation. Samples R and I, representing the two species at localities about 80 miles apart in northern Sinaloa, are slightly less different, especially in five characters that are discussed below. The largest individuals of *P. artus* occur in this area adjacent to the range of *P. goldmani*. The size of the jugal (character 23) is correlated with over-all size. The exoccipital flange (character 27) and the size of the stylomastoid foramen (character 28) are correlated with each other and to a lesser extent with larger size. Characters 21 and 22 are correlated with each other and are probably not a result of larger size. The five characters involve, therefore, the size and configuration of the lacrimal, in which regard sample R of *P. artus* is less different from *P. goldmani* than other samples of *P. artus*. If intergradation were occurring such would be expected. At least two other possible explanations exist, however. Also, sample R is quite distinct from samples of *P. goldmani* and agrees with other samples of *P. artus* in other characters, a condition that would not be expected in case of intergradation. If the environment of the coastal plain of northern Sinaloa and Sonora favored larger size and a certain lacrimal configuration, these features might have arisen separately in the two species in adjacent areas. Another possibility is that the two species, although now distinct and not interbreeding, have been

derived from a single species which had geographic variation that has persisted in the separate species. These two possibilities (post-speciational persistence of an earlier pattern of geographic variation and post-speciational origin of a similar pattern) are each more probable than the third explanation—intergradation.

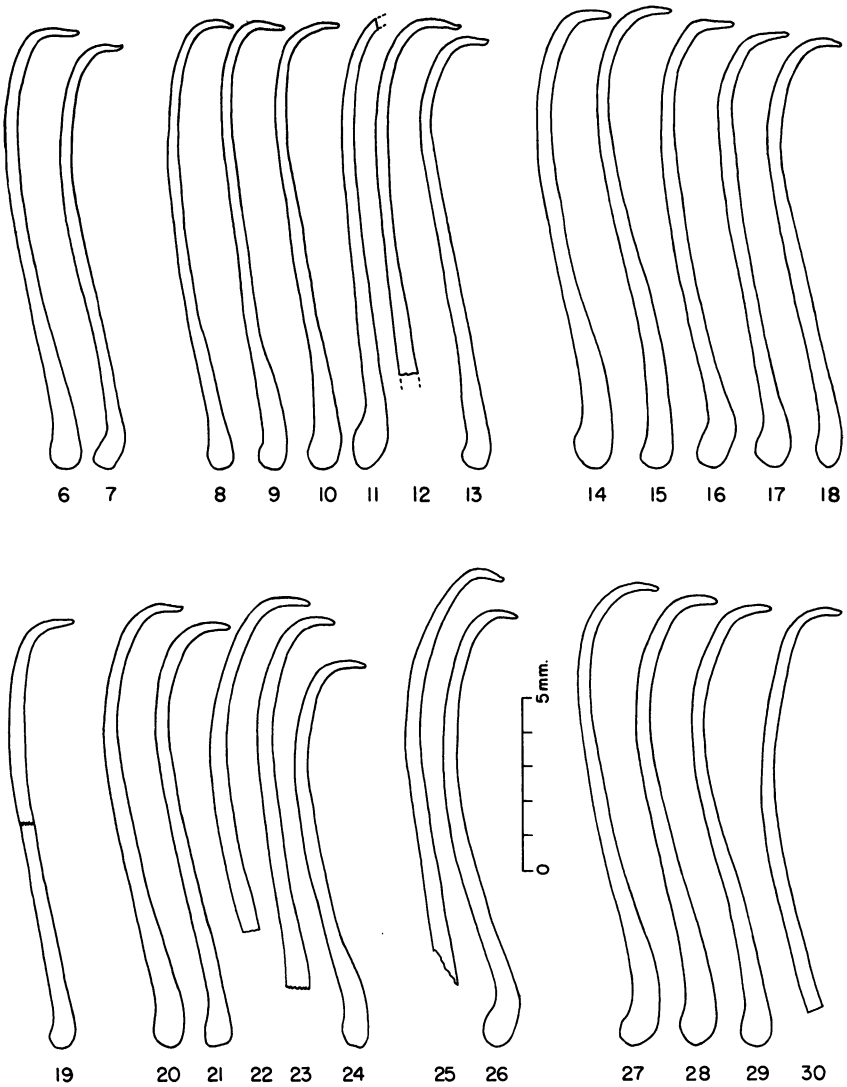
The two forms are now known to occur together and to remain distinct at five different localities, and to occur only 1 mile apart at another locality. The five localities at which both forms have been captured are: Carimechi, Chihuahua; 4 miles northwest of Alamos, Sonora; Alamos, Sonora; 3 miles northeast of El Fuerte, Sinaloa; and 8 kilometers north and 22 kilometers east of Sinaloa, Sinaloa (see fig. 2).

In southern Sonora the geographic ranges of the two forms overlap by at least 30 miles, *P. artus* occurring as far west as Chinobampo and *P. goldmani* occurring as far east as 10 miles southeast of Alamos.

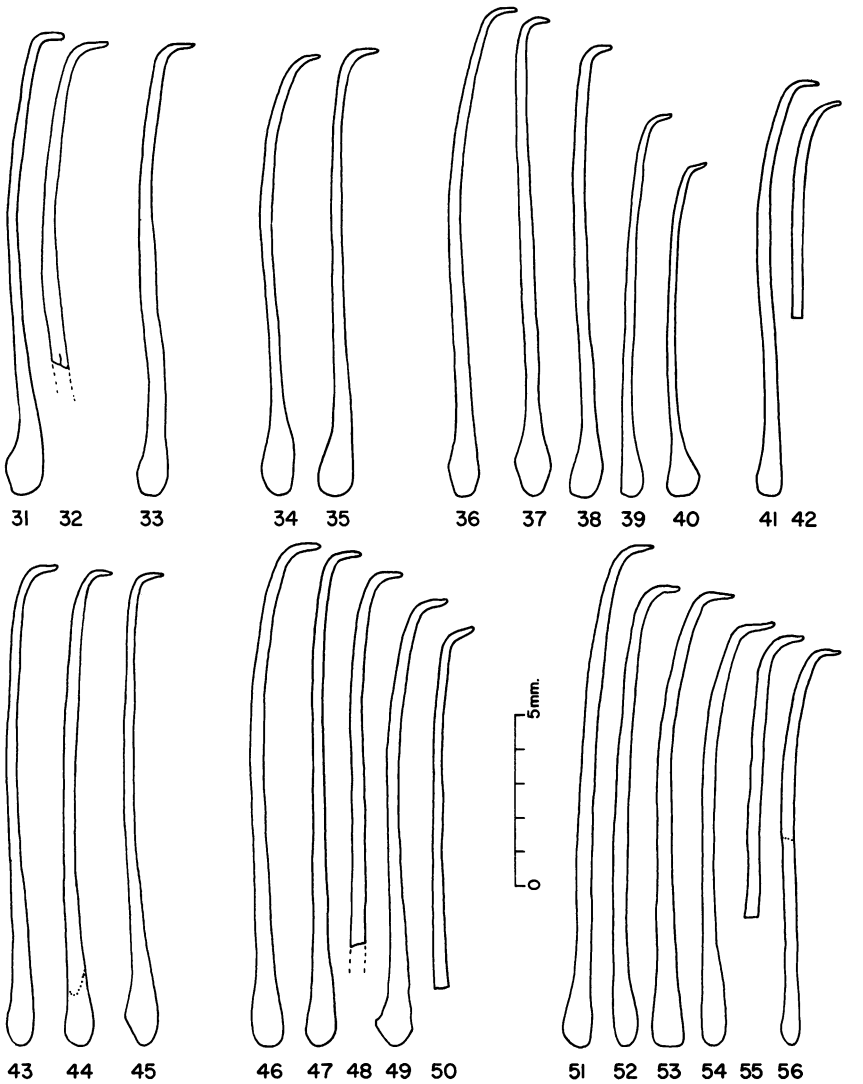
All specimens that I have examined are clearly referable to one form or the other. I conclude that *P. artus* and *P. goldmani* are distinct species.

The ecological requirements, tolerances, and differences between two species that are as closely related as *P. artus* and *P. goldmani* are of interest, but have not been studied. Decreasing humidity from southeast to northwest along the coastal plain of western Mexico, and a shift from the coast back toward the sierras of the less xeric tropical vegetation have been commented upon in connection with the distributional pattern of neotropical bats in this area (Anderson, 1960, p. 8). The shift of the range of *P. artus* back from the coast in the northern part of the range of the species, and the replacement of *P. artus* by *P. goldmani* on the coastal plain, are correlated with the shift of humidity and vegetation. The topography of the area occupied by *P. artus* in the northern part of its range is more mountainous, and the soils are in general rocky rather than sandy. Data are at present inadequate to lead to any conclusion in regard to the relative effects of humidity, vegetation, and soil upon these pocket mice. Possibly these two species displace each other ecologically to some extent where they occur together; little information is available on this subject.

The following synonymies document the nomenclatorial and bibliographic histories of these pocket mice. The number of specimens listed here from certain localities differs from numbers reported by previous authors. Therefore, the lists of specimens examined include catalogue numbers so as to eliminate doubt as to what specimens are here listed. There are additional specimens that are in liquid preservative or that were not prepared at the time of my study at the University of Kansas and the University of Michigan. These specimens are not listed here.



FIGS. 6–30. Bacula of specimens of *Perognathus artus* from seven localities. Bacula from each locality are grouped together. Catalogue numbers are listed in the text. The localities beginning in the upper row from left to right are: Urique, Chihuahua (two specimens); Vado Cuchujachi, 9 miles east-southeast of Alamos, Sonora (six); 4 miles north of Terrero, Sinaloa (five); and in the lower row, 40 miles northwest of Culiacan, Sinaloa (one); 1 mile south of Pericos, Sinaloa (five); 12 miles north of Culiacan, Sinaloa (two); and 32 miles south-southeast of Culiacan, Sinaloa (four). These series of bacula are illustrated to show some of the variation with age (extremely young specimens are not shown) and also individual variation. The occurrence of characters diagnostic of the species throughout its range is also shown.



FIGS. 31–56. Bacula of specimens of *Perognathus goldmani* from eight localities. Bacula from each locality are grouped together. Catalogue numbers are listed in the text. The localities beginning in the upper row from left to right are: 1 mile east of Buena Vista, Sonora (two specimens); ½ mile north of La Aduana, Sonora (one); 10 miles southeast of Alamos, Sonora (two); 33 miles south-southeast of Navojoa, Sonora (five, arranged from older to younger, and illustrating persistence of diagnostic features); 2½ miles north of El Fuerte, Sinaloa (two); and, in the lower row, 3 miles north and 1 mile east of San Miguel, Sinaloa (three); 10 miles north-northwest of Los Mochis, Sinaloa (five); and 13 miles north-northeast of Los Mochis, Sinaloa (six).

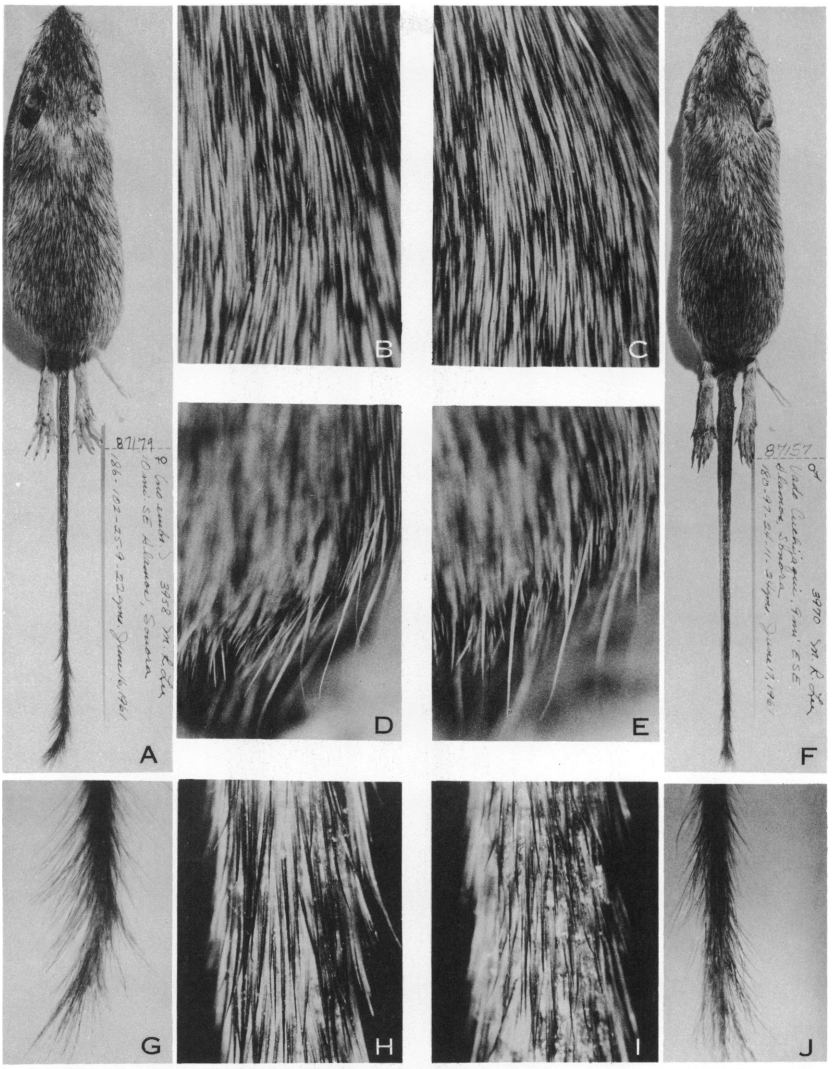


FIG. 57. Comparison of external characters of *Perognathus artus* (K.U. No. 87157, right half of page) and *Perognathus goldmani* (K.U. No. 87179, left half of page). A, F. Entire specimens. × ½. B, C. Enlargements of parts of dorsal pelage to illustrate the slightly more "blended" appearance of *P. artus*. D, E. Enlargements of the right part of the rump to show the slightly finer and less abundant spines of *P. artus*. G, J. Enlargements of the tips of tails to show shorter and less numerous hairs of *P. artus*. H, I. Enlargements of a middle part of each tail to show the paler, slenderer, and less numerous hairs and consequently more visible annular scales of *P. artus*. Photographs A and F are by Alexander Rota. Enlargements are from photographs by the author.

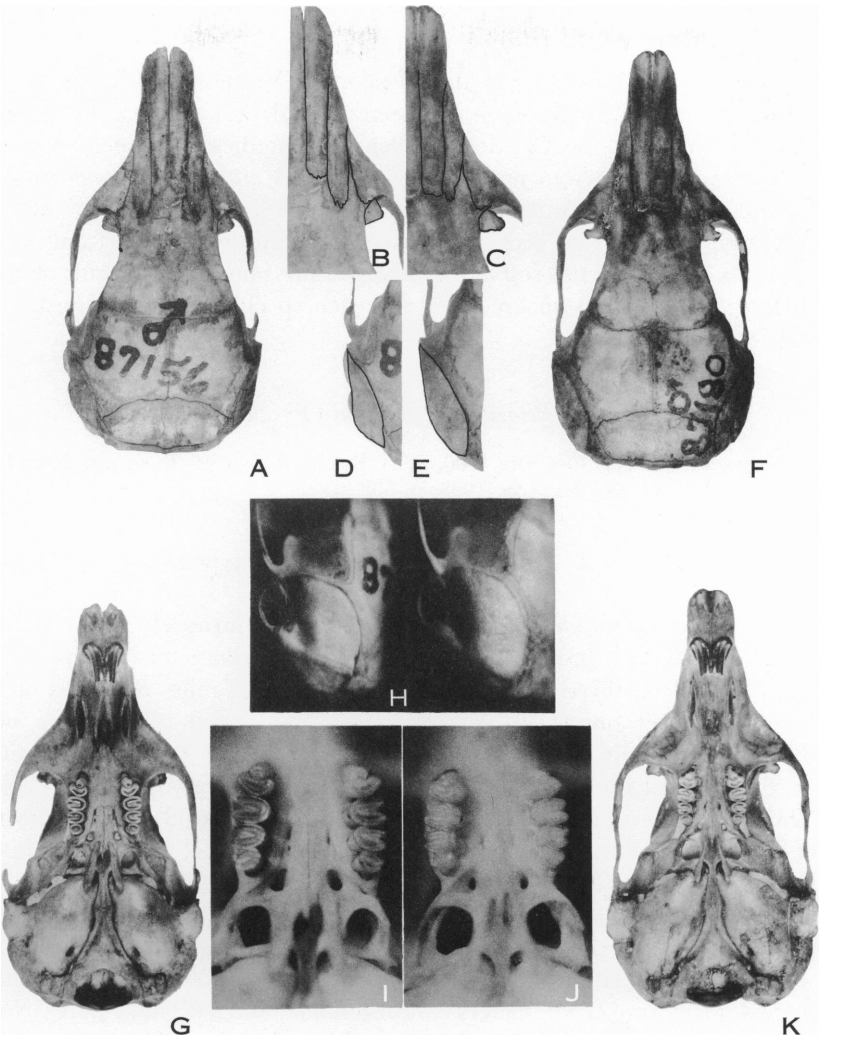


FIG. 58. Comparison of cranial characters of *P. artus* (left half of page) and *P. goldmani* (right half of page). All photographs are of the same pair of skulls. A, F. Dorsal views. ×2. G, K. Ventral views. ×2. B, C. Slightly greater enlargements of anterior part of skull to show longer premaxillary, less attenuate lacrimal, and more posterior position of maxillo-frontal suture relative to the base of the lacrimal. D, E, H. Smaller and less "inflated" mastoidal part of the bulla and the more conspicuous stylomastoid foramen of *P. artus*. I, J. Larger posterior palatal pits and foramina of *P. artus*. Other cranial differences noted in text are also shown. The two specimens shown are from males of comparable maturity from localities only about 1 mile apart. At other places, as noted in the text, both species occur together. H, I, and J are from photographs by the author; others were photographed in ultraviolet light by Robert Logan.

More than 250 specimens in the Museum of Vertebrate Zoology at the University of California have not been studied by me, but I have been advised (verbally) by Dr. Seth B. Benson that these specimens provide no evidence contrary to my conclusion that *P. artus* and *P. goldmani* are distinct species. Localities are arranged in the lists first by state, alphabetically, and then by geographic position within each state from north to south. Localities not separately mapped are noted. The bacula shown in figures 6 through 56 are listed for each species, following the list of specimens examined.

Perognathus goldmani Osgood

Perognathus goldmani OSGOOD, 1900, p. 54. BURT, 1938, p. 45. BURT AND HOOPER, 1941, p. 6. HALL AND KELSON, 1959, p. 502.

Perognathus goldmani goldmani: HALL AND OGILVIE, 1960, p. 516.

The type specimen is U.S.N.M. No. 96673. The type locality is Sinaloa, Sinaloa.

SPECIMENS EXAMINED: Total, 238. *Chihuahua:* Carimechi, two (U.M.-M.Z. Nos. 83130, 83131). *Sinaloa:* Laguna, 17 kilometers southwest of Choix, 500 feet, three (K.U. Nos. 89365–89367); 8 miles northeast of El Fuerte, 200 feet, one (U.I. No. 12522); 2½ miles north of El Fuerte, not mapped separately from El Fuerte, 16 (K.U. Nos. 75277–75292); 3 miles northeast of El Fuerte, 200 feet, not mapped separately, one (K.U. No. 89373); El Fuerte, four (K.U. Nos. 75293–75295, 75298); 2 miles north of San Blas, 50 feet, six (K.U. Nos. 89387, 89389–89392, 89396); 13 miles north-northeast of Los Mochis, 13 (U.I. Nos. 12489, 12490, 12507–12517); 3 miles north and 1 mile east of San Miguel, not mapped separately from preceding locality, four (K.U. Nos. 85121–85124); 10 miles north-northwest of Los Mochis, 19 (K.U. Nos. 61388, 61389, 61392–61408); 8 kilometers north and 22 kilometers east of Sinaloa, 400 feet, nine (K.U. Nos. 90233–90236, 90238, 90240–90243); Sinaloa, seven (U.S.N.M. Nos. 96668–96674); 1 mile east of Sinaloa, 180 feet, not mapped separately from Sinaloa, 16 (K.U. Nos. 90248–90255, 90257–90264); 1 mile north of Topolobampo, 50 feet, five (K.U. Nos. 89398, 89399, 89401–89403); 1 mile northwest of Topolobampo, not mapped separately from preceding locality, two (K.U. Nos. 89404, 89405); 16 kilometers southeast of Topolobampo, 120 feet, two (K.U. Nos. 90269, 90270). *Sonora:* Presa Obregón, 150 feet, one (K.U. No. 90196); 1 mile east of Buena Vista, on Río Yaqui Reservoir, 1000 feet, not mapped separately from Presa Obregón, two (K.U. Nos. 80049, 80050); 25 miles northwest of Navojoa, four (U.I. Nos. 12518, 12593, 12594, 12603); Camoa, Río Mayo, about

800 feet, 16 (U.C.L.A. Nos. 19016, 19017, 19045–19047, and U.S.N.M. Nos. 95812–95817, 96323–96328); 41 kilometers east-northeast of Navojoa, 400 feet, not mapped separately from Camoa, six (K.U. Nos. 90199–90202, 90207, 90208); 6.7 miles north and 17.3 miles east of Navojoa, not mapped separately from Tesia, two (U.A. 3984, 3986); Tesia, 17 (A.M.N.H. Nos. 172077–172079, and U.C.L.A. Nos. 16963, 16964, 16998, 17007, 17009, 18147, 18162, 18229, 18231, 18240–18243); 12 miles west-northwest of Alamos, two (U.I. Nos. 12629, 12634); 8 miles west-northwest of Alamos, not mapped separately from the preceding locality, two (U.I. Nos. 12627, 12628); ½ mile north of La Aduana, not mapped separately from the preceding two localities, three (U.A. Nos. 3972, 3974, 3975); 1 mile west of Alamos, not mapped separately from Alamos, two (U.I. Nos. 12635, 12636); Alamos, 54 kilometers east of Navojoa [approximately 4 miles by road northwest of Alamos according to field notes of the collector], not mapped separately from Alamos, about 1000 feet, 26 (K.U. Nos. 89310–89314, 89316–89321, 89325–89330, 89337, 89338, 89341–89347); Alamos, 12 (U.S.N.M. Nos. 96306, 96307, 96310–96316, 96318, 96321, 96322); 4½ miles southeast of Alamos, 1000 feet, not mapped separately, five (K.U. Nos. 80051–80055); 10 miles southeast of Alamos, nine (K.U. Nos. 87176–87184); 3 miles north-northwest of Bacabachi, two (K.U. Nos. 69699, 69701); 33 miles south-southeast of Navojoa, 12 (U.I. Nos. 12493–12500, 12519–12521, 12585); 33½ miles south-southeast of Navojoa, not separately mapped, five (U.I. Nos. 12491, 12492, 12568–12570).

The bacula of specimens having the following catalogue numbers are shown in figures 31 through 56 in the order here listed: K.U. Nos. 80050, 80049; U.A. No. 3974; K.U. Nos. 87177, 87180; U.I. Nos. 12498, 12496, 12494, 12495, 12585; K.U. Nos. 75287, 75285, 85124, 85123, 85122, 61403, 61406, 61398, 61407, 61393; U.I. Nos. 12490, 12512, 12489, 12510, 12513, and 12515.

Perognathus artus Osgood

Perognathus artus Osgood, 1900, p. 55. Burt, 1936, p. 151; 1938, p. 46. Burt and Hooper, 1941, p. 6. Hall and Kelson, 1959, p. 503.

Perognathus goldmani artus: Hall and Ogilvie, 1960, p. 517.

Perognathus goldmani Osgood, 1900, p. 55, misidentification of six specimens from Alamos, Sonora. Burt, 1938, p. 46, misidentification of one specimen from Chinobampo, Sonora; 1960, p. 42, pl. 11, specimens from Guirocoba, Sonora.

The type specimen is U.S.N.M. No. 96298. The type locality is Batopilas, Chihuahua.

Specimens Examined: Total, 316. *Chihuahua:* Carimechi, Río Mayo,

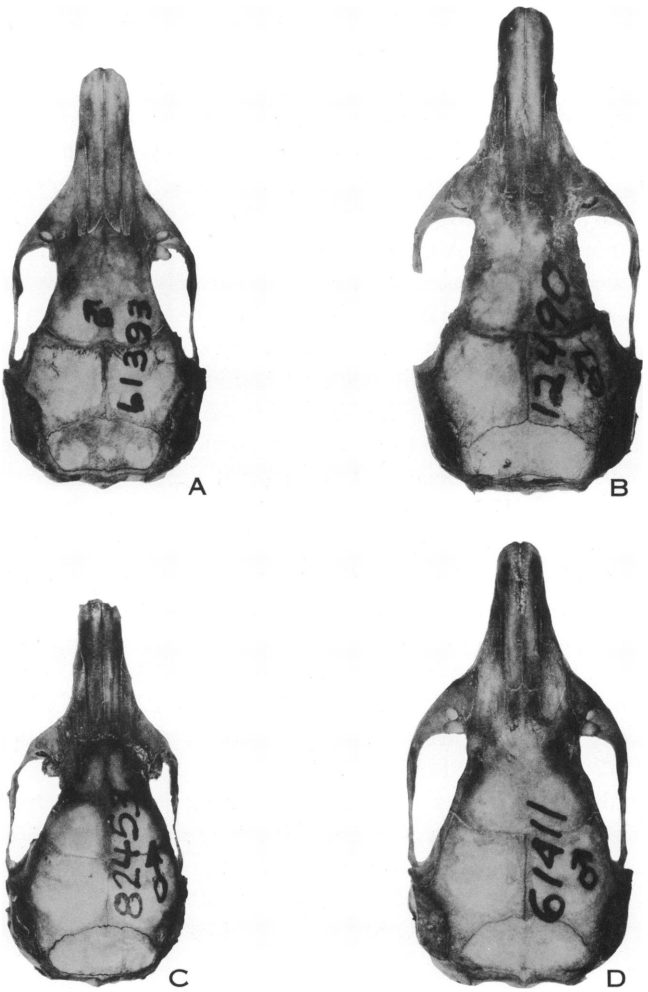


FIG. 59. Skulls of adult males. A. *Perognathus goldmani*, K.U. No. 61393, from 10 miles north-northwest of Los Mochis, Sinaloa. B. *P. goldmani*, U.I. No. 12490, from 13 miles north-northeast of Los Mochis, Sinaloa. C. *P. artus*, K.U. No. 82453, from Urique, 1700 feet, Chihuahua. D. *P. artus*, K.U. No. 61411, from 4 miles north of Terrero, Sinaloa. The range in size of adult males is shown. A and C show skulls that are among the smallest of each species; B and D, those that are among the largest. The relatively greater mastoidal breadth and some other distinctive characters of *P. goldmani* are shown. Photographs are by Robert Logan and were made in ultraviolet light. $\times 2$.

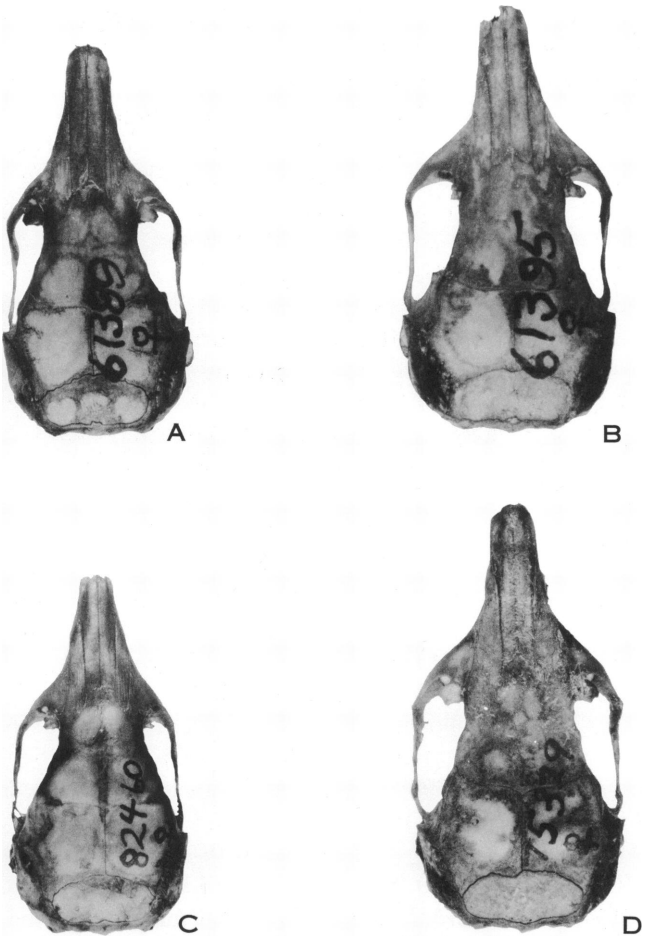


FIG. 60. Skulls of adult females. A, B. *Perognathus goldmani*, K.U. Nos. 61389 and 61395, respectively, both from 10 miles north-northwest of Los Mochis, Sinaloa. C. *P. artus*, K.U. No. 82460, from Urique, 1700 feet, Chihuahua. D. *P. artus*, K.U. No. 75329, from 6 miles north and 1½ miles east of Eldorado, Sinaloa. A and C show skulls that are among the smallest of each species; B and D, those that are among the largest. A comparison of this figure with figure 59 will show that the minimum and maximum sizes of females are smaller than those of males in both species. Photographs are by Robert Logan and were made in ultraviolet light. ×2.

eight (U.M.M.Z. Nos. 83122–83129); 3 miles northeast of Temoris, 5600 feet, three (K.U. Nos. 81153–81155); Urique, 1700 feet, 24 (K.U. Nos. 82437–82460); 1½ miles southwest of Tocuina, 1500 feet, 11 (K.U. Nos. 79517–79527); 40 kilometers north and 6 kilometers west of Choix, 2400 feet, not mapped separately from locality near Tocuina, three (K.U. Nos. 90822–90824); Batopilas, about 2500 feet, two (U.S.N.M. Nos. 96297, 96298); "near Batopilas," about 2800 feet, six (U.S.N.M. Nos. 96299–96304). *Durango:* Chacala, 564 meters, three (U.S.N.M. Nos. 96675, 96684, 96693). *Sinaloa:* Twenty-six miles northeast of Choix, four (K.U. Nos. 75273–75276); 18 kilometers north-northeast of Choix, two (K.U. Nos. 89351, 89353); 16 kilometers north-northeast of Choix, 1700 feet, not mapped separately from preceding locality, eight (K.U. Nos. 89354–89359, 89362, 89364); 3 miles northeast of El Fuerte, 200 feet, 10 (K.U. Nos. 89368–89372, 89374, 89375, 89383, 89384, 89386); 44 kilometers east-northeast of Sinaloa, 600 feet, 10 (K.U. Nos. 90209, 90211–90217, 90223, 90224); 8 kilometers north and 22 kilometers east of Sinaloa, three (K.U. Nos. 90230, 90231, 90237); 40 miles northwest of Culiacan, one (U.I. No. 12523); 4 miles north of Terrero, seven (K.U. Nos. 61409–61415); 12.1 miles north of Pericos, not mapped separately from the preceding locality, five (U.I. Nos. 13185–13189); 1 mile south of Pericos, 24 (K.U. Nos. 61444, 61454, 61456, 61458–61461, 61464, 61467–61470, 61473, 61476–61486); 13.4 miles north of Culiacan, not mapped separately from the following locality, one (U.I. No. 13190); 12 miles north of Culiacan, 42 (K.U. Nos. 67653–67657, 67659–67680, 67682, 67684–67694, 67696–67698); 16 miles northwest of Culiacan, 500 feet, 16 (U.M.M.Z. Nos. 109418–109433); Culiacan, 175 feet, four (U.S.N.M. Nos. 96676–96678, 96680); 32 miles south-southeast of Culiacan, 19 (K.U. Nos. 61488, 61489, 61504, 61513, 61515, 61523, 61528, 61534, 61540, 61542, 61551–61555, 61557–61560); 6 miles north and 1½ miles east of Eldorado, 40 (K.U. Nos. 75302–75307, 75309–75342); Piaxtla, one (K.U. No. 69753); Mazatlan, one (A.M.N.H. No. 13766); "near Mazatlan" [=9 miles southeast of Mazatlan], nine (U.S.N.M. Nos. 96682, 96685–96692); 2 miles west of Villa Union, one (K.U. No. 39922); Escuinapa, one (A.M.N.H. No. 24520); 21.8 miles northwest of Acaponeta, Nayarit, in Sinaloa, one (U.I. No. 13191); Pinos Gordo, 4500 feet [exact location unknown, not mapped], one (U.M.M.Z. No. 75266). *Sonora:* Alamos, 54 kilometers east of Navojoa [=4 miles northwest of Alamos], two (K.U. Nos. 89315, 89333); Alamos, six (U.S.N.M. Nos. 96305, 96308, 96309, 96317, 96319, 96320); 11 miles east of Alamos, one (U.A. No. 6318); 11.3 miles east of Alamos, Rio Cuchujachi, 1200 feet, not separately mapped, five (U.A. Nos. 1984–1987, 6350); Vado

Cuchujachi, 9 miles east-southeast of Alamos, not separately mapped, 18 (K.U. Nos. 87154–87162, 87164–87166, 87168–87173); 9 miles southeast of Alamos, two (K.U. Nos. 80056, 80057); Chinobampo, one (U.C. L.A. No. 18204); Guirocoba, 30 miles southeast of Alamos, 1450 feet, 10 (U.C.L.A. Nos. 18305, 18307, 51088, 51089, 51101, 51111–51113, 51115, 51116).

The bacula of specimens having the following catalogue numbers are shown in figures 6 through 30 in the order here listed: K.U. Nos. 82440, 82449, 87154, 87162, 87156, 87159, 87157; U.A. No. 1985; K.U. Nos. 61411, 61412, 61409, 61410, 61413; U.I. No. 12523; K.U. Nos. 61481, 61479, 61464, 61485, 61483, 67656, 67659, 61557, 61513, 61488, and 61504.

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